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Phenotypic plasticity, global change, and the speed of adaptive evolution.

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Highlights :
3 to 5 bullet points (maximum 85 characters, including spaces, per bullet point)

- Phenotypic plasticity can influence the rate of evolution of insects
- The rate of evolution will depend on how plasticity alters the strength of selection
- The response to selection will also depend on plasticity alters trait correlations
- More studies are needed to address this question in insects

Abstract (100-200 mots)
Faced with a rapidly changing environment, phenotypic plasticity allows for the production of a diversity of intra-generational responses, but the subsequent consequence inter-generational evolutionary processes is still difficult to predict. In this article, we review theory and empirical studies addressing this question in insects by considering three scenarios. Adaptive plasticity that should lead to slow or no evolution. Non-adaptive phenotypic plasticity to new environmental conditions that should lead either to extinction or, on the contrary, to rapid evolutionary change. The third scenario deals with how plasticity alters the variance selection acts upon. These scenarios are then discussed by highlighting the effects of genetic correlations between phenotypes. We conclude that more studies are needed in insects to better understand the relationship between phenotypic plasticity and evolutionary processes.

Introduction

The first response of organisms to environmental change is often through plasticity in behavior, physiology, or other environmentally sensitive traits [1–3]. Such plasticity is by definition a non-evolutionary response to the environment, because it occurs within the generation of an individual. However, a long-standing question in evolutionary biology is whether the plasticity observed within generations influences subsequent evolutionary change

across generations [1–3]. Understanding the relationship between plasticity and evolution has taken on increased importance in the context of rapid global change as historic patterns of temperature and rainfall are simultaneously changing in a directional manner and showing increased variability [4,5].

Insects, like other ectotherms exhibit plasticity in a suite of traits related to temperature (reviewed in [5]), and because of their relatively fast generation times also have the potential to rapidly evolve [6]. Insect populations are therefore good models for considering the relationship between plasticity and evolution. For example, the life cycles of insects living at higher latitudes have evolved plastic responses to specific environmental cues that help them survive cold winters, but climate change is increasingly disrupting the reliability of these cues [5]. How might this disruption alter patterns of plasticity and subsequent evolutionary change? Our goal here is to provide possible answers to this question by reviewing evolutionary theory and presenting different scenarios for how plasticity will alter the rate of adaptive evolution. Where possible, we use empirical studies of insects as examples to illustrate these concepts.

The evolutionary response of a trait to an episode of selection is dependent on the strength of directional selection and the amount of genetic variance [7]. Thus, understanding how plasticity impacts the heritability or additive genetic variance/covariance for a trait, and the strength of selection should allow for predicting the rate of evolutionary change in a population. Indeed, a traditional perspective is that plasticity slows the rate of evolutionary change because most of the phenotypic variance is environmentally induced and non-heritable [3]. Under such conditions even strong selection will fail to produce an evolutionary response. However, it is now generally accepted that plasticity is itself a trait that exhibits genetic variation and has the capacity to evolve [8]. If plasticity itself is heritable, then a critical question becomes how a particular environment alters the distribution of phenotypes within a population relative to the optimal phenotype (e.g. [1–3].). We focus on three scenarios: 1) adaptive plasticity, where the environment predictably shifts the distribution of phenotypes towards the optimum, 2) non-adaptive plasticity, where the environment predictably shifts the distribution of phenotypes away from the optimum, and 3) effect on variance, where the environment alters the range of variance available for selection to act on (reviewed in [3]). Below we expand on these ideas in more detail and the implications for insects dealing with global change.

I Adaptive Plasticity

Adaptive plasticity is used here in the sense of beneficial plasticity, i.e. that allows individuals to have a higher fitness in the new environment than it would be if not plastic [3,9,10]. There are many examples of adaptive phenotypic plasticity in insects. In butterfly species, seasonal plasticity (i.e. polyphenism - [11]) with regard to adult colour pattern [12–15] has received considerable attention and was shown to be adaptive [16–20]. Another well documented example is the case of diapause induction, the cessation of reproduction and/or suppressed metabolism as a strategy to persist through harsh conditions (reviewed in [5]).

In the event of a rapid change in the environment, adaptive phenotypic plasticity is hypothesized to allow organisms to 1) adaptively modify traits over a very short (intra-generational) timescale, 2) assist in the initial survival of populations, and 3) reduce the probability of extinction [21]. While this hypothesis has been the subject of much modelling work [22–26], it has received very little empirical evidence at this time. However, comparisons of phenotypic plasticity in invasive and native populations have been used to address this

question. Such studies are abundant in plants with mixed results [27]. In insects, the degree to which adaptive plasticity benefits to the first step of the invasion starts to be studied in *Drosophilids* [28] and in particular on the morphology of the wing, a very temperature sensitive trait that can evolve quickly and is probably adaptively [29,30]. For example, Loh et al [31] found significantly different plastic responses to temperature in the wing size of Brazilian vs African populations of *Zaprionus indianus*. Fraimout et al. [32] found that wing plasticity was associated to an effect on flight speed but did not find any significant differences in wing morphology plasticity between three populations of *Drosophila suzukii*.

How should adaptive plasticity influence the rate of adaptive evolution? If the phenotype is close to the optimum, then directional selection will be weak and the population should evolve slowly or not at all unless there is a substantial fitness cost to plasticity [1,3,33]. Quantitative genetic approaches [7] can be used to determine the optimum phenotype and the strength of selection. Another strategy is to compare the reaction norms of populations occupying different environments. If adaptive phenotypic plasticity weakens selection, then there should be little genetic differentiation between populations. For example, Ayrinhac et al. [34] compared populations of *Drosophila melanogaster* for chill coma recovery time, a very plastic trait depending on developmental temperature, and found the adaptive variation arose from phenotypic plasticity, not genetic differentiation. Similar conclusions have been obtained on other traits in *Drosophila* [35–38] and in some other species [39,40] but in many studies, this question is generally not specifically addressed, especially in the case of non-linear reaction norm.

II. Non-Adaptive Phenotypic Plasticity

While natural selection has led to the evolution of adaptive plasticity, not all plastic responses to the environment are adaptive. We define non-adaptive plasticity as an environmentally-induced change that shifts the phenotype further away from the phenotypic optimum [3,41]. Under such a definition, non-adaptive plasticity is not beneficial in terms of individual fitness. At the population level, the presence of non-adaptive plasticity is most likely to be found under novel environmental conditions where past selection has not had an opportunity to act on the genetic variation for plasticity [3]. Non-adaptive plasticity has two potential evolutionary outcomes. The first potential outcome is the extinction of the population. Extinction is always a possible outcome in response to a rapid or strong episode of selection, and any non-adaptive plastic response should exacerbate this possibility, particularly if the trait(s) involved are closely tied to fitness [23]. A second potential outcome is rapid adaptive evolution (e.g. [42]. Non-adaptive plasticity can facilitate rapid evolution by increasing the strength of selection, and given the presence of sufficient genetic variation, lead to adaptive changes in either the trait or the reaction norm of the trait [42,43]. In such a scenario, non-adaptive plasticity may be a transient phenomenon that is important during the early stages of adaptation when the difference between the plastic response and the local optimum are greatest and the strength of selection strongest. However, determining what the local optimum for any phenotype is, and the degree to which any given environment is really novel are challenging problems when attempting to assess non-adaptive phenotypic plasticity.

In the context of global change, the critical question is: how often might insect populations exhibit non-adaptive plasticity? In theory, two scenarios are expected to generate non-adaptive plastic responses to the environment: 1) countergradient selection, and 2) extreme environmental conditions (heatwaves, prolonged droughts, cold-snaps, etc..) that lie outside the historic range of

environmental conditions. Countergradient selection describes situations where the plastic response to the environment is non-adaptive or in the opposite direction favored by selection, resulting in genetic compensation or cryptic adaptation [44–46]. Conover et al. [45] review such cases and find numerous insect examples across temperature gradients associated with latitude or elevation. For example, high latitude insect populations are under selection for faster growth rates in response to colder temperature, but the plastic response to cold temperatures is slower growth leading to adaptive evolution for faster growth rates in high relative to low latitude populations (reviewed in [45]). Extreme environments outside the range of historic conditions may also generate non-adaptive plasticity because selection has not had the opportunity to shape the plastic response (e.g. [3]). Insects may be particularly sensitive to such extreme climate events, particularly at high latitudes where populations have evolved physiological and life-history traits to survive cold winters (see [5]). For example, warmer autumn temperatures may not sufficiently prepare insects physiologically to survive cold winter temperatures [47,48], while warmer winter temperatures may cause non-adaptive early emergence from diapause leading to higher mortality [48,49].

III. Stressful environmental conditions and phenotypic variation

A classic tenet of ecological genetics – largely based upon laboratory studies on *Drosophila* – is that stressful environmental conditions tend to increase phenotypic variation [50,51]. As adaptation depends on the existence of heritable variation ($R = h^2S$, where R is the response to selection, S is the selection differential and h^2 is heritability), this effect might have deep evolutionary consequences, and in particular it may influence the adaptability to ongoing global changes. In the previous examples of adaptive and non-adaptive plasticity we focused largely on changes in S. However, stressful conditions can also potentially induce increased heritability ($h^2=V_A/V_P$, where V_A is additive genetic variance and V_P the total phenotypic variance), if the increased phenotypic variance is genetically based. A higher heritability and response to selection could boost the adaptive potential to the new stressful conditions. Alternatively, if the increased variance is not genetically based, an increase in V_P would in turn decrease heritability, reducing the evolutionary potential. The generality of the stress-induced increase in variation has nevertheless been seriously questioned in the past two decades [52,53]. Can we identify a general effect of stress upon genetic variation and what can insects studies tell us about it?

The interest for stress-induced variation may be traced back to Waddington's experiments with *Drosophila* [54]. He showed that stressors such as heat shocks or ether vapor could elicit a burst of phenotypic variation upon which artificial selection could be successfully applied. The evolutionary response demonstrated that the elicited variation was indeed genetic – but conditional to the environmental stress. Such storage and release of cryptic genetic variation and their molecular bases have since received much attention (e.g. [55–58]). In particular, the work on Hsp90 in *Drosophila* [56] has shown that a wide range of cryptic genetic variants could be stored and conditionally released. The induced variation is however generally detrimental (Figure 1B; [56,59,60]) and whether it could contribute to adaptive evolution has been controversial (e.g. [61]).

The hypothesis that stress induces an increase in genetic variation is not universally supported. Hoffmann and Merilä [53] were the first to challenge the generality of this hypothesis. Later, Charmantier and Garant [52] reported in a meta-analysis that heritability rather tends to increase under *favorable* conditions. This discrepancy with the early *Drosophila* laboratory

studies was discussed in terms of environmental novelty. In natural populations, stressful conditions would be the norm rather than the exception, while the stressors exerted in lab conditions would often represent completely new conditions. Many studies since then have explored the effects of extreme and novel environmental conditions on genetic variation for various traits, producing contrasting results. Among insects, a few *Drosophila* studies have reported an increase in genetic variation with stressful temperature [62–64] or larval crowding [65]. High temperature was found to reveal cryptic genetic variation in a female sperm storage organ in a sepsid fly [66]. Drought stress increased additive genetic variation for wing size and melanization in a butterfly species [67]. Edvardsson et al [68] detected a strong increase in additive genetic variation for ovarian apoptosis in starved cockroach females. In contrast, other studies failed to detect such effect: for example, in *Drosophila*, genetic variation for heat resistance was not affected by drought stress [69] and neither was genetic variation for viability by temperature [70]. A recent meta-analysis based on 39 studies (including 11 on insects) suggests no consistent effect of stressful conditions for morphology, while life history traits tend to present higher genetic variation under stress [71]. Altogether, these results suggest that although genetic variation is clearly dependent on the environment, the effect of stress is likely trait, taxon and environment specific.

Discussion

The exact relationship between plasticity and evolution can be difficult to predict, but our perspective here is that by focusing on how plasticity alters the strength of selection and the amount of genetic variation expressed, predictions can be made about the rate of evolution. We summarize this perspective in a pair of conceptual figures (Figures 1 & 2). We can conceptualize the relationship between plasticity and adaptive evolution using a modified view of Fisher [72] and Orr's [73] geometric model of adaptation (Figure 1).

Rather than considering the distributional effects of mutations on the adaptive walk towards a local optimum, we can instead consider the effects of plasticity on a fitness landscape (following [3]). Collectively, the perspective presented here argues that predicting if insects will evolve in response to climate or any other environmental change requires qualitatively or quantitatively estimating how the plastic responses alter the strength of selection. We recognize this is challenging, but not impossible. For example, numerous studies to date have asked whether patterns of plasticity in thermal tolerance are adaptive and sufficient to buffer populations under future climate scenarios [5].

The scenarios depicted in Fig. 1 assume plasticity as a univariate response, however, adaptation to changing environments is more likely to be a multivariate process involving numerous genetically correlated traits. The G-matrix or genetic variance-covariance matrix is a statistical tool for quantifying trait correlations [7,74] and can be visualized as an ellipse [75,76], whose axes represent the main directions of available genetic variation. Such trait correlations can either constrain the evolutionary response to selection if the selection gradient is orthogonal to the major axis of variation or facilitate the evolutionary response if selection is along the major axis [75,76]. However, there is also considerable evidence that trait correlations are plastic [77–79], and thus could influence the evolutionary response to selection. We depict some of these outcomes in Figure 2, using a stable fitness landscape as in Figure 1.

In summary, phenotypic plasticity in a diversity of traits will be the first response of organisms to environmental change, and these plastic responses will in turn have implications for

how populations evolve by altering the strength of selection and amount of expressed genetic variation. Yet, few studies have explored the linkages between plasticity and evolution in natural populations of insects. We argue that more studies should explicitly test such linkages to better improve long-term projections of how insect populations will perform under future climate scenarios.

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References

Papers of particular interest, published within the period of review, have been highlighted as:
• of special interest
•• of outstanding interest

1. Price TD, Qvarnström A, Irwin DE: **The role of phenotypic plasticity in driving genetic evolution.** *Proc Biol Sci* 2003, **270**:1433–40.

2. Paenke I, Sendhoff B, Kawecki TJ: **Influence of Plasticity and Learning on Evolution under Directional Selection**. *Am Nat* 2007, **170**:E47–E58.

3. * Ghalambor CK, McKay JK, Carroll SP, Reznick DN: **Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments**. *Funct Ecol* 2007, **21**:394–407.

4. ** Hoffmann AA, Sgrò CM: **Climate change and evolutionary adaptation**. *Nature* 2011, **470**:479–485.

5. ** Sgrò CM, Terblanche JS, Hoffmann AA: **What Can Plasticity Contribute to Insect Responses to Climate Change?** *Annu Rev Entomol* 2016, **61**:433–452.

6. Loxdale HD: **Rapid genetic changes in natural insect populations**. *Ecol Entomol* 2010, **35**:155–164.

7. Lande R, Arnold SJ: **The Measurement of Selection on Correlated Characters**. *Evolution (N Y)* 1983, **37**:1210–1226.

8. Scheiner SM: **Genetics and Evolution of Phenotypic Plasticity**. *Annu Rev Ecol Syst* 1993, **24**:35–68.

9. Gotthard K, Nylin S, Nylin S: **Adaptive Plasticity and Plasticity as an Adaptation: A Selective Review of Plasticity in Animal Morphology and Life History**. *Oikos* 1995, **74**:3.

10. * Schmid M, Guillaume F: **The role of phenotypic plasticity on population differentiation**. *Heredity (Edinb)* 2017, doi:10.1038/hdy.2017.36.

11. Shapiro A: **Seasonal polyphenism**. *Evol Biol* 1976, **9**:259–333.

12. Windig JJ: **Reaction norms and the genetic basis of phenotypic plasticity in the wing pattern of the butterfly Bicyclus anynana**. *J Evol Biol* 1994, **7**:665–695.

13. Koch P, Brakefield P, Kesbeke F: **Ecdysteroids control eyespot size and wing color pattern in the polyphenic butterfly Bicyclus anynana (Lepidoptera: Satyridae).** *J Insect Physiol* 1996, **42**:223–230.

14. Roskam JC, Brakefield PM: **10 E hl Seasonal polyphenism in Bicyclus (Lepidoptera : Satyridae) butterflies : different climates need different cues**. 1999,

15. Mateus ARA, Marques-Pita M, Oostra V, Lafuente E, Brakefield PM, Zwaan BJ, Beldade P: **Adaptive developmental plasticity: Compartmentalized responses to environmental cues and to corresponding internal signals provide phenotypic flexibility**. *BMC Med* 2014, **12**:1–15.

16. Kingsolver JG: **Fitness consequences of seaonal polyphenism in westen white butterflies**. *Evolution* 1995, **49**:942–954.

17. Brakefield PM: **Seasonal polyphenism in butterflies and natural selection**. *Trends Ecol Evol* 1996, **11**:275–276.

18. Kemp DJ, Jones RE: **Phenotypic plasticity in field populations of the tropical butterfly Hypolimnas bolina (L .) (Nymp halidae)**. *Biol J Linean Soc* 2001, **72**:33–45.

19. Hazel WN: **The environmental and genetic control of seasonal polyphenism in larval color and its adaptive significance in a swallowtail butterfly**. *Evolution (N Y)* 2002, **56**:342–348.

20. Stoehr A, Goux H: **Seasonal phenotypic plasticity of wing melanisation in the cabbage white butterfl y , Pieris rapae L . (Lepidoptera : Pieridae)**. *Ecol Entomol* 2008, **33**:137–143.

21. Pigliucci M: *Phenotypic plasticity. Beyond nature and nurture.* Johns Hopkins University Press; 2001.

22. Lande R: **Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation**. *J Evol Biol* 2009, **22**:1435–1446.

23. ** Chevin L, Lande R, Mace GM: **Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory**. *PLoS Biol* 2010, **8**:e1000357.

24. * Ashander J, Chevin L, Baskett ML, Ashander J: **Predicting evolutionary rescue via evolving plasticity in stochastic environments**. 2016,

25. Scheiner SM, Barfield M, Holt RD: **The genetics of phenotypic plasticity . XV . Genetic assimilation , the Baldwin effect , and evolutionary rescue**. 2017, **7**:8788–8803.

26. Nunney L: **Adapting to a changing environment: modeling the interaction of directional selection and plasticity**. *J Hered* 2016, **107**:15–24.

27. Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M: **Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions.** *Ecol Lett* 2006, **9**:981–93.

28. Gibert P, Hill M, Pascual M, Plantamp C, Terblanche JS, Yassin A, Sgrò CM: **Drosophila as models to understand the adaptive process during invasion**. *Biol Invasions* 2016, **18**:1089–1103.

29. Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L: **Rapid evolution of a geographic cline in size in an introduced fly.** *Science* 2000, **287**:308–9.

30. Nunney L, Cheung W: **The Effect of Temperature on Body Size and Fecundity in Female Drosophila melanogaster: Evidence for Adaptive Plasticity**. *Evolution (N Y)* 1997, **51**:1529–1535.

31. Loh R, David JR, Debat V, Bitner-Mathá BC: **Adaptation to different climates results in divergent phenotypic plasticity of wing size and shape in an invasive drosophilid.** *J Genet* 2008, **87**:209–217.

32. Fraimout A, Jacquemart P, Villarroel B, Aponte DJ, Decamps T, Herrel A, Cornette R, Debat V: **Phenotypic plasticity of *Drosophila suzukii* wing to developmental temperature: implications for flight**. *J Exp Biol* 2018, **221**:jeb166868.

33. Crispo E: **Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow**. *J Evol Biol* 2008, **21**:1460–1469.

34. Ayrinhac A, Debat V, Gibert P, Kister A-G, Legout H, Moreteau B, Vergilino R, David JR: **Cold adaptation in geographical populations of Drosophila melanogaster: phenotypic plasticity is more important than genetic variability**. *Funct Ecol* 2004, **18**:700–706.

35. Gibert P, Huey RB: **Chill-coma temperature in Drosophila: effects of developmental temperature, latitude, and phylogeny**. *Physiol Bioch Zool* 2001, **74**:429–434.

36. Liefting M, Hoffmann AA, Ellers J: **Plasticity versus environmental canalization: population differences in thermal responses along a latitudinal gradient in Drosophila serrata.** *Evolution* 2009, **63**:1954–63.

37. Klepsatel P, Gáliková M, De Maio N, Huber CD, Schlötterer C, Flatt T: **Variation in thermal performance and reaction norms among populations of drosophila melanogaster**. *Evolution (N Y)* 2013, **67**:3573–3587.

38. Hoffmann A, Shirriffs J, Scott M: **Relative importance of plastic vs genetic factors in adaptive differentiation: geographical variation for stress resistance in Drosophila melanogaster from eastern Australia**. *Funct Ecol* 2005, **19**:222–227.

39. Wool D, Hales DF: **Phenotypic Plasticity in Australian Cotton Aphid (Homoptera : Aphididae): Host Plant Effects on Morphological Variation**. 1997,

40. Ragland GJ, Kingsolver JG: **The effect of fluctuating temperatures on ectotherm life-history traits : comparisons among geographic populations of Wyeomyia smithii**. *Evol Ecol* 2008,

41. Morris M, Rogers S: **Overcoming maladaptive plasticity through plastic compensation**. *Curr Zool* 2013, **59**:526–536.

42. Ghalambor CK, Hoke KL, Ruell EW, Fischer EK, Reznick DN, Hughes K a.: **Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature**. *Nature* 2015, doi:10.1038/nature15256.

43. Chevin L-M, Gallet R, Gomulkiewicz R, Holt RD, Fellous S: **Phenotypic plasticity in evolutionary rescue experiments.** *Philos Trans R Soc Lond B Biol Sci* 2013, **368**:20120089.

44. Conover D, Schultz ET: **Phenotypic similarity and the evolutionary significance of countergradient variation**. *Trends Ecol Evol* 1995, **10**:248–252.

45. Conover DO, Duffy TA, Hice LA: **The Covariance between Genetic and Environmental Influences across Ecological Gradients Reassessing the Evolutionary Significance of Countergradient and Cogradient Variation**. *year Evol Biol* 2009, **1168**:100–129.

46. Grether GF, CUmmings ME, Hudon J: **Countergratient variation in the sexual coloration of guppies (Poecilia reticulata): Drosopterin synthesis balances carotenoid availability**. *Evolution (N Y)* 2005, **59**:175–188.

47. Coleman P, Bale JS, Hayward S: **Cross-generation plasticity in cold hardiness is associated with diapause, but not the non-diapause developmental pathway, in the blow fly Calliphora vicina**. *J Exp Biol* 2014, **217**:1454–1461.

48. Stuhldreher G, Hermann G, Fartmann T: **Cold-adapted species in a warming world – an explorative study on the impact of high winter temperatures on a continental butter fl y**. *Entomol Exp Appl* 2014, **151**:270–279.

49. Bale JS, Hayward S: **Insect overwintering in a changing climate**. *J Exp Biol* 2010, **213**:980–994.

50. Hoffmann AA, Parsons PA: *Extreme Environmental Change and Evolution*. Cambridge University Press.; 1997.

51. Hoffmann AA, Parsons PA: *Evolutionary genetics and environmental stress*. Oxford University Press; 1991.

52. Charmantier A, Garant D: **Environmental quality and evolutionary potential: Lessons from wild populations**. *Proc R Soc B Biol Sci* 2005, **272**:1415–1425.

53. Hoffmann AA, Merilä J: **Heritable variation and evolution under favourable and unfavourable conditions**. *Trends Ecol Evol* 1999, **14**:96–101.

54. Waddington C: **Canalization of development and the inheritance of acuired characters**. *Nature* 1942, **150**:563–565.

55. Gibson G, Hogness DS: **Drosophila Regulatory Gene Ultrabithorax on Homeotic Stability**. *Science (80-)* 1996, **271**:200–203.

56. Rutherford SL, Lindquist S: **Hsp90 as a capacitor for morphological evolution**. *Nature* 1998, **6709**:336–342.

57. Gibson G, Dworkin I: **Uncovering cryptic genetic variation**. *Nat Rev Genet* 2004, **5**:681.

58. Paaby AB, Rockman M V.: **Cryptic genetic variation: Evolution's hidden substrate**. *Nat Rev Genet* 2014, **15**:247–258.

59. Wagner GP, Chiu CH, Hansen TF: **Is Hsp90 a regulator of evolvability?** *J Exp Zool* 1999, **285**:116–118.

60. Masel J: **Cryptic genetic variation is enriched for potential adaptations**. *Genetics* 2006, **172**:1985–1991.

61. * McGuigan K, Sgrò CM: **Evolutionary consequences of cryptic genetic variation**. *Trends Ecol Evol* 2009, **24**:305–311.

62. Swindell WR, Bouzat JL: **Reduced inbreeding depression due to historical inbreeding in Drosophila melanogaster: Evidence for purging**. *J Evol Biol* 2006, **19**:1257–1264.

63. Sisodia S, Singh BN: **Variations in morphological and life-history traits under extreme temperatures in Drosophila ananassae**. *J Biosci* 2009, **34**:263–274.

64. van Heerwaarden B, Malmberg M, Sgrò CM: **Increases in the evolutionary potential of upper thermal limits under warmer temperatures in two rainforest Drosophila species**. *Evolution (N Y)* 2016, **70**:456–464.

65. Horváth B, Kalinka AT: **Effects of larval crowding on quantitative variation for development time and viability in Drosophila melanogaster**. *Ecol Evol* 2016, **6**:8460–8473.

66. Berger D, Walters RJ, Blanckenhorn WU: **Experimental evolution for generalists and specialists reveals multivariate genetic constraints on thermal reaction norms**. *J Evol Biol* 2014, doi:10.1111/jeb.12452.

67. Talloen W, Van Dongen S, Van Dyck H, Lens L: **Environmental stress and quantitative genetic variation in butterfly wing characteristics**. *Evol Ecol* 2009, **23**:473–485.

68. Edvardsson M, Hunt J, Moore AJ, Moore PJ: **Quantitative genetic variation in the control of ovarian apoptosis under different environments**. *Heredity (Edinb)* 2009, **103**:217–222.

69. Bubliy OA, Kristensen TN, Kellermann V, Loeschcke V: **Humidity affects genetic architecture of heat resistance in Drosophila melanogaster**. *J Evol Biol* 2012, **25**:1180–1188.

70. Ketola T, Kellermann V, Kristensen TN, Loeschcke V: **Constant, cycling, hot and cold thermal environments: Strong effects on mean viability but not on genetic estimates**. *J Evol Biol* 2012, **25**:1209–1215.

71. ** Rowiński PK, Rogell B: **Environmental stress correlates with increases in both genetic and residual variances: A meta-analysis of animal studies**. *Evolution (N Y)* 2017, **71**:1339–1351.

72. Fisher R: *The genetical theory of natural selection*. [date unknown].

73. Orr HA: **The Population Genetics of Adaptation: The Distribution of Factors Fixed during Adaptive Evolution**. *Evolution (N Y)* 2006, **52**:935–949.

74. Lande R: **Quantitative Genetic Analysis of Multivariate Evolution , Applied to Brain : Body Size Allometry**. *Evolution (N Y)* 1979, **33**:402–416.

75. Steppan SJ, Phillips PC, Houle D: **Comparative quantitative genetics: evolution of the G matrix**. *Trends Ecol Evol* 2002, **17**:320–327.

76. Schluter D: **Adaptive Radiation Along Genetic Lines of Least Resistance**. *Evolution (N Y)* 1996, **50**:1766–1774.

77. Andersen JL, Manenti T, Sørensen JG, MacMillan H a., Loeschcke V, Overgaard J: **How to assess Drosophila cold tolerance: chill coma temperature and lower lethal temperature are the best predictors of cold distribution limits**. *Funct Ecol* 2015, **29**:55–65.

78. Wood CW, Brodie ED: **Environmental effects on the structure of the G-matrix**. *Evolution (N Y)* 2015, **69**:2927–2940.

79. Sgrò CM, Hoffmann AA: **Genetic correlations, tradeoffs and environmental variation**. *Heredity (Edinb)* 2004, **93**:241–248.

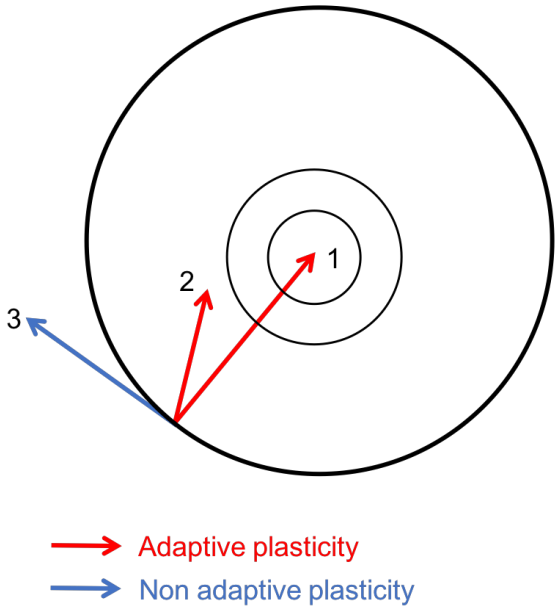
Figure Legends

Figure 1 – When adaptive plasticity results in a perfect match with the optimum (Fig. 1a1), there is no opportunity for directional selection and thus no evolutionary change is predicted. When adaptive plasticity reduces the mismatch between the phenotype produced and the optimum (Fig. 1a2), there is an opportunity for directional selection can act, but we would predict a weaker evolutionary response and the rate of adaptive evolution to be slower. In contrast, because non-adaptive plasticity increases the mismatch between the expressed phenotype and the optimum (Figure 1a3), the strength of directional selection is increased and should result in either rapid adaptive evolution or extinction. In cases where the environment induces a release of genetic variation (Figure 1b) we expect a range of non-adaptive and adaptive responses and selection to favor those genotypes that produce the most adaptive responses.

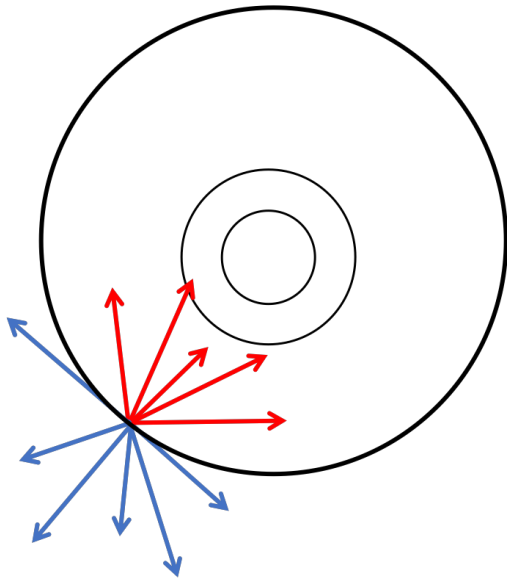
Figure 2 - Considering a population where the major axis of genetic variation is orthogonal to the direction of the local optimum (Figure 2a), we would predict the evolutionary response to be slow and follow a trajectory that is biased by the major axis. In contrast, plasticity in trait correlations can lead to diversity of outcomes that might influence evolutionary responses. For example, plasticity could re-orient the major axis towards the phenotypic optimum, facilitating adaptive evolution (Figure 2b-1). Alternatively, plasticity could shift both the orientation and the location of the matrix, such that trait combinations are closer to the local optimum (Figure 2b-2,3), but differ in their orientation (Figure 2b-2,3). Lastly, plasticity may simply increase the variance (Figure 2b-4).

Figure 1

a



b

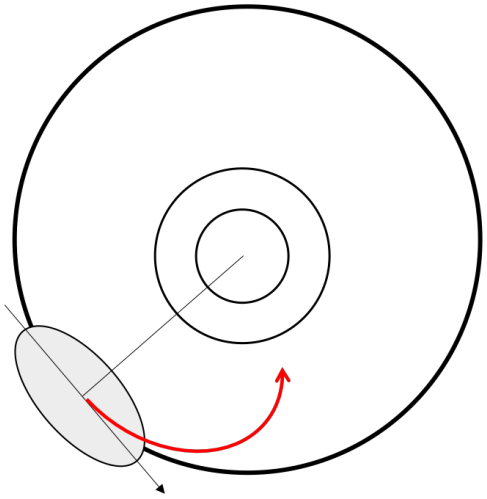


Adaptive plasticity

Non adaptive plasticity

Figure 2

a



Evolutionary trajectory

b